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Defining and designing plant architectural ideotypes to control epidemics?

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Abstract Ideotypes are a popular concept for plant breeders, who designate as such the ideal combinations of traits in a particular genotype to reach a pre-set production objective within a given socio-economic context. The historical, 'genetic' view of ideotypes has been more recently extended to cover the design of plant genotypes for specific cropping systems (the 'agronomic' view), or even the ideal combination of parameters, identified from formal or simulation modeling, to a specific agronomic problem (the 'modelling' view). These different forms of ideotypes in turn lead to different strategies for breeding plants. This paper will briefly describe, analyse and discuss some applications of these ideotype views, using the specific case of architectural traits of plant and crop canopies to limit the epidemic development of pests and diseases in crops. It is not intended to be an exhaustive

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and objective review of the existing literature on plant ideotypes, but rather to express as an 'opinion' paper the views discussed and elaborated among participants to the EpiArch network.

Keywords Conception · Model · Expert knowledge · Optimization · Plant architecture · Annuals · Trees · Epidemiology · Ideotype · Canopy

Every farmer dreams about '<u>the</u> perfect plant': the one that, when grown in his farm's environment, would give the highest attainable yield and quality. This dream has fueled the efforts to breed better genotypes, and led plant scientists (mainly geneticists and later agronomists) to coin the concept of 'ideotype' in order to identify the best traits to combine into such a perfect plant (Donald 1968; Parker et al. 2003).

While yield and quality remain the ultimate objectives for growers, these targets are severely constrained by a wide array of pests and pathogens. It is therefore quite surprising that the quest of ideotypes has only rarely been applied to design plants which could prevent or limit the epidemiological development of diseases or pests by characteristics other than tissue resistance to infection, most notably their shape and/or growth dynamics (Coyne et al. 1974; Schwartz et al. 1978; Le May et al. 2009). Therefore, a multidisciplinary think-tank, involving plant protection specialists, plant geneticists, agronomists, and modellers, was organized within INRA (the French National Institute for Agronomic Research) as a scientific network called EpiArch, in order to analyse, formalize and elaborate the research questions that need to be addressed to tackle this objective. The present concept paper summarizes the views developed during two one-day EpiArch seminars, involving the scientists within EpiArch and several 'end-users' of ideotypes, about ideotypes in general and the possibilities, shortcomings and consequences of developing some based on plant architecture and suitable for the low-input, high performance cropping systems now required to sustainably feed the world (Tillman et al. 2002). In particular, it describes which qualities such an ideotype requires, which multidisciplinary approaches can be followed to design it, and, finally, how to combine different traits to breed a plant that would be accepted by both farmers and consumers.

Ideotypes: what and what for?

Plant and canopy architectures are, at least in some pathosystems, powerful levers to limit inoculum production, inoculum dispersion and/or inoculum efficacy, and thus contribute to slow down epidemic progress (see Ando et al. 2007; Tivoli et al. 2012). It also can contribute to change the susceptibility of organs or to favour mechanisms leading to infection escape or to increased tolerance (Ney et al. 2012). While architecture has a strong genetic component (e.g. Bendokas et al. 2012), it can also be manipulated through elements of the crop production system (see Lauri and Laurens 2005; Calonnec et al. 2012; Simon et al. 2012). This makes it possible, at least from a theoretical point of view, to design and build plants or canopies that will minimize the epidemic potential of one or more pests.

Once this possibility is recognized, the next question that immediately comes forward is 'how to identify which traits to combine for optimal performance?' This question brings forward the concept of 'ideotype', first defined as 'biological model[s] … expected to perform or behave in a predictable manner within a defined environment' (Donald 1968). This original definition relates to phenotypes of individual plants, and to the combination of the appropriate alleles/QTLs suitable to generate them under given growth conditions. It was later extended to the combination of plant genotypes and plant management actions (e.g. pruning - Lauri and Laurens 2005; Simon et al. 2006, 2012) or cropping systems (e.g. organic agriculture) to achieve specific performances (Ellissèche et al. 2002; van Bueren et al. 2002), and then further still to the phenotypes of crop canopies rather than of single plants (e.g. Lawless et al. 2005; Brunel-Muguet et al. 2011).

An ideotype can only be defined relative to one objective and/or to one set of constraints and opportunities. While the objective is open for definition, the constraints set the field of possible solutions and therefore, the opportunities for optimization. Among the main constraints are the range (sometimes limited) of genetic or plastic (i.e., epigenetic) variability available within the species considered, but also the socio-economic preoccupations that impose strong limitations to acceptable solutions. For instance, mixing resistant and susceptible cultivars of small grains (wheat, barley, etc.…) is highly efficient to limit the spread of aerial fungal diseases like rusts or powdery mildews; part of this limiting effect is due to the presence of physical barriers to plant-to-plant infection (Finckh et al. 2000), and hence to architectural modifications of the crop canopy. Such mixtures can therefore be regarded as ideotypes for grain production with low or no fungicide input. However, they often fail to be adopted in practice, because end-users are often reluctant to process mixtures of which they do not master the precise composition (Wolfe 1985). So, because the set of constraints are different for each of the two practitioners, the same mixture can be a perfect ideotype for the plant disease epidemiologist, and a poor one for the maltster. Similarly, the rice mixture grown with great success in China to prevent the severe yield losses to rice blast, caused by *Magnaporthe grisea*, with minimal fungicide input (Zhu et al. 2000) would not be an acceptable ideotype if the hand labour necessary to harvest separately the strips of waxy and non-waxy cultivars was not available at a low hourly cost. The same constraint (high hand labour necessary to manage the orchard) prevents within-row mixtures of apple trees with different susceptibilities to apple scab, caused by the ascomycete *Venturia inaequalis*, from being an acceptable ideotype in conventional agriculture, although they do reduce the epidemic spread of this major disease (Didelot et al. 2007).

The conceptual dimensions of ideotypes

Being a concept initially coined by and for plant breeders, ideotypes carry an obvious genetic dimension: which optimal combination of genes (or QTLs) to build to obtain the desired phenotypes? However, this genetic view was rapidly complemented by an agronomic view, when ideotypes began to be thought as the plant component of a cropping system. Because, as we have seen above, ideotypes can only be defined relative to a production objective, they also bear a clear socio-economic dimension, especially regarding their acceptability: a plant type that would not be adopted by growers could hardly be ideal! Finally, ideotypes are basically virtual prototypes of plants not existing at the time they are designed. As such, they are conceptual models, that may or may not be formalized mathematically but which in all cases are based on sets of decision rules upon which the choice of traits to assemble and the optimal combinations of these can be decided.

These four dimensions (genetic, agronomic, modelling and socio-economic) are all legitimate, but can sometimes be strongly conflicting. A good example of the necessity to reconcile all of these dimensions in a successful ideotype is given by the case of apple trees resistant to scab through the resistance gene *Rvi6* (formerly known as *Vf*). Many resistant apple cultivars were bred in various countries throughout the world, without meeting a commercial success until recently – with the French cv. Ariane. These cultivars fitted an ideotype targeting one demand – to grow apples with a strongly reduced use of pesticides. This target was fully justified from an environmental point of view, but did not meet a societal demand – and hence a market – until the recent move towards low input, sustainable agriculture and the national action plans elaborated in many European countries to drastically lower the amount of pesticides sprayed on crops (Freier and Boller 2009). The thorough analysis of the difficulties faced by scab-resistant cultivars to meet a market (Vanloqueren and Baret 2004) illustrates that a co-design of ideotypes by geneticists, agronomists and end-users is critical to ensure their success.

How should then one deal with the multiple dimensions of ideotypes: look for a (maybe non-optimal) compromise, or make strong choices favouring one view over all others? We believe that an ideotype is basically a virtual, intermediary object (Vinck and Jeantet 1995), useful to formulate, confront, and sometimes reconcile, the visions of specialists from different interacting disciplines. The plurality of conceptual dimensions relative to ideotypes also reflects the plurality of optimization solutions to reach a particular goal, and hence the plurality of ideotypes themselves (see for example Donald 1968; Dickman 1985; Dickman et al. 1994). In this sense, ideotypes are neither blueprints/robot pictures of a 'wannabe' cultivar, nor sheer utopia, but formal, explicit tools to design multidisciplinary solutions to practical problems, to assess their operational potential and limitations, and therefore to choose between competing designs (see Boujut and Blanco 2003, for a similar approach in engineering design). As such, they do not necessarily lead to the direct breeding of actual cultivars, although they often do: rather they may be a step in formalizing new desirable trait combinations – in other terms, new plant types (e.g. Khush 1995; Karlsson Strese et al. 1996). Up to now, ideotypes were most often defined for only one objective, usually disciplinary, without considering other objectives or views. We argue here that successfully defining an ideotype requires combining different points of view and matching different qualities, first of which the best agronomic features for the farmer and the best acceptability for the end-users.

Designing ideotypes

There are two main ways to design ideotypes. The first is to start from the existing (already available cultivars in particular, but also current cropping systems) and modify those incrementally towards new, and hopefully better, genotypes (or cropping systems). This method is very close to the standard operation of breeding activities, and relies on gradual changes rather than complete redesign. It is usually directly fueled by expert knowledge which provides a synthetic, if sometimes empirical, picture of the ideotype itself. Because of the incremental way in which plant traits are modified in this strategy, such ideotypes are often adaptations of existing cultivars, and therefore are faced with few issues about practical acceptance by end-users. They are however ill-suited to major changes in objectives (for instance a 50 % reduction in pesticide use), and do not generate plant types that are radically new, such as a C-4 instead of a C-3 rice plant (von Caemmerer et al. 2012).

An alternative way of designing ideotypes is thus to start from the objective itself, and identify 'out of the blue' (i.e., with no regard of what is already existing) the best possible genotype to achieve it. This method, which is liable to generate highly unusual solutions, often takes advantage from the use of models which can be used for simulation and/or for optimization (see for instance Haverkort and Grashoff 2004; Qi et al. 2010; Quilot-Turion et al. 2011; Suriharn et al. 2011; Milo and Last 2012). Such models (see Casadebaig et al. 2012 for an example about plant architecture and epidemic control) can include a complete redesign of the plants, and can integrate genetic, agronomic and other types of constraints (Sylvester-Bradley et al. 2012).

Interestingly, these models sometimes lead to generate new variables that can serve as novel traits to breed for. A prime example is canopy porosity, which can be defined as 'the ratio of pore space to the space occupied by plant organs' (Tivoli et al. 2012; Calonnec et al. 2012). Porosity can be manipulated as a single, 'black box' variable in a model, which sensitivity analysis shows to be a major architectural determinant in the performance of crops to escape or limit infection (Casadebaig et al. 2012). However, because porosity is the end-result of the interplay of different architectural features - which are not necessary the same for different plants (Table 1) - it is not easily phenotyped. The model-assisted ideotype design would therefore require to devise new phenotyping protocols, preferably high-throughput and operable in 'standard' field canopies rather than on isolated plants or small plots, before variation for this trait can be quantified, analyzed (including with respect to genotype × environment × cropping system interactions) and eventually exploited in breeding. The conception of new ideotypes able to limit disease progress may thus impose the need to revisit the germplasm collections and screen them for phenotypical features which either escaped breeding operations for want of appropriate assessment methods, or were traded-off for yield productivity or for other adaptative traits with high economic value.

Theory-oriented models based on concepts from ecology or evolution can also be used to generate ideotypes through this strategy (Weiner et al. 2010). In this case, the model is used to make theoretical predictions and compare broad plant types rather than individual genotypes, but the rationale remains the same: use *in silico* experiments to screen among possibles, before actually engaging any breeding activities.

The use of methods from the field of multi-objective optimization algorithms, in conjunction with complex plant models, is of particular interest since these methods provide the decision-maker with a set of diversified solutions among which to choose. This is just starting, and the corresponding pioneering studies of Letort et al. (2008), Qi et al. (2010) and Quilot-Turion et al. (2011) open the way to further consideration of various cropping system scenarios and climatic environments, as well as the genetic components in the models (Quilot-Turion et al. 2011).

Architectural ideotypes to limit disease and pest progress

When designing ideotypes to limit disease spread, and given the very large differences between pathosystems, there might seem at first that there is little hope to go beyond a set of case studies and identify some generic, favourable architectural traits. However, the design of a generic, process-based model (Casadebaig et al. 2012), and its confrontation with experimental data from five, strikingly different, aerial pathosystems of annual and

Table 1 Architectural traits unfavourable to epidemic development in selected pathosystems, and their contribution to three integrative variables (canopy porosity, vigour, senescence). The status of each trait (e.g. "low", "erect"....) having a negative effect on epidemic development for each pathosystem was determined according to published evidence; status in italics indicate that the effect is postulated, but not demonstrated yet

Architectural trait	Pathosystem					Integrative variables		
	Pea Ascochyta blight	Yam anthracnose	Grapevine powdery mildew	Apple scab[1]	Potato late blight	Porosity	Vigour	Senescence
Organ topology and geometry								
Foliar size	Small				*Small*	√	√	
Internode length	*Long*				*Long*	√		
Spacing between foliar and fruiting organs			*Large*	Large		√		
Stem firmness	High					√		
Stem density				Low	*Low*	√	√	
Secondary ramification	*Low*		Low			√	√	√
Growth dynamics								
Plant shape	*Erect*	*Erect*		Spreading		√		
Canopy closure[2]	Slow			Low & slow	*Slow*	√		√
Leaf area index (LAI)	Small		*Small*	Small	*Small*	√	√	√
Leaf area density (LAD)		*Low*	*Low*	Low	Low	√	√	
Earliness		Early	*Early*				√	√
Ontogenic resistance[3]		*Early*	*Early*	Early				√

[1] defined at the scale of the tree, rather than the whole orchard

[2] within one cropping season. For all pathosystems, this trait relates to the speed of canopy closure; in apple scab, it also includes the degree of canopy closure within a tree at the peak of the season

[3] Ontogenic resistance is included in this table because this physiological trait can be strongly influenced by canopy architecture (shading, leaf emission rythm, etc.…)

perennial plants reveals that some key integrative variables emerge, notably canopy porosity, canopy vigour and plant senescence (Table 1).

Most of these variables can then be broken down into separate traits directly accessible to phenotyping, such as leaf area index, stem number, distances between organs, leaf density, etc.… Some of these traits, by themselves or in combination, have pleiotropic effects on one or more integrative variables, and will therefore act simultaneously on processes different by nature: for instance, canopy closure, LAI and a high level of ramifications will all have pleiotropic effects on porosity and on senescence. Such pleiotropic traits would prove very good targets for breeding – or for canopy management - as soon as their effects on epidemiological processes are clear (see Calonnec et al. 2012). However, a closer examination of Table 1 shows that the status of most traits is still to be confirmed experimentally in most pathosystems, and may be of no or limited impact in some of them. This shows that a generic model can be useful to conceive ideotypes, but that the validation of such ideotypes will require experimental data rather than by simulations only. The model therefore acts as a sieve among many possibilities, and helps to limit the experimental validation work to the most promising combinations. It also directs attention to specific research (e.g., 'are erect potato genotypes less susceptible to late blight spread?') to confirm the generic nature of postulated relationships deduced from observations in other pathosystems.

Finally, it is important to point out that some of the traits favourable for disease limitation (for instance few stems and small foliar areas) might impose a trade-off with other desirable characteristics, such as productivity. This illustrates the fact that an ideotype is always designed relative to one objective. Changing this objective (for instance, shifting from 'designing a potato architectural ideotype able to limit late blight spread' to 'designing a potato architectural ideotype limiting late blight spread while allowing an average yield of 50 t/ha in western Europe' or to 'designing a potato architectural ideotype limiting late blight spread in organic crops') will result in markedly different plants (Ellissèche et al. 2002). The final validation of ideotypes derived from models therefore comes not from the breeder or the agronomist, but from the end-user. Therefore, the objective against which ideotypes are to be designed needs to be a multi-criterion one if acceptability is to be ensured. This justifies both the importance of expert knowledge at some stage in ideotype design, and the fact that the initial specifications the ideotype is to meet is a crucial step in the design process itself.

Where to now?

Model-assisted design of ideotypes imposes conceptual and methodological advances, most notably about the definition and evaluation of integrative variables. It however provides a very useful tool to manage complex interactions (for instance the pleiotropic actions of architectural traits on several epidemiological processes) and, therefore, to favour the necessary interdisciplinary exchange that ideotype design requires. However, at the moment, most process-based models (such as the generic model elaborated by Casadebaig et al. 2012) still lack a strong, explicit integration of the genetic determinants of architecture traits, and therefore do not allow yet to take full advantage of the rapid advances in high-throughput biology (phenomics and genomics particularly).

A major step forward has been made when the concept of ideotype was extended from single plants to whole canopies. The current trends towards greater integration within agricultural design now motivates ideotype designers to think about plant canopy ideotypes within cropping system ideotypes – i.e. to envisage the plant as one component of the cropping system, rather than as the product of this system. This broader view may lead to a re-evaluation the design system itself, using innovative design theories which redefine – and sometimes re-invent - the functions of objects (Hatchuel and Weil 2009). In a world where constraints are rapidly changing, it is crucial that ideotypes no longer be ideal objects cast in stone, but rather intellectual guidelines to achieve specific goals.

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